

VARIABILITY IN GROWTH OF HARD CLAMS, *MERCENARIA MERCENARIA*¹

ARNOLD G. EVERSOLE
DEPARTMENT OF AQUACULTURE, FISHERIES AND WILDLIFE
and
LAWRENCE W. GRIMES
EXPERIMENT STATISTICS UNIT
CLEMSON UNIVERSITY
CLEMSON, SOUTH CAROLINA 29631 U.S.A.
and
PETER J. ELDRIDGE
NATIONAL MARINE FISHERIES SERVICE
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
CHARLESTON LABORATORY
CHARLESTON, SOUTH CAROLINA 29400 U.S.A.

ABSTRACT

Growth and survival of hard clams, *Mercenaria mercenaria* (L.), were determined for 13-month old individuals grown for 4.5 years in protected trays in a subtidal site in South Carolina. Calculated annual mortality rate was 4%. Most growth (change in shell length, SL) occurred in the first 2 years. Growth appeared to be a function of age and size with younger clams of the same size growing faster than older clams. Similarly, smaller clams grew faster than larger clams of the same age. The smaller clams were consistently faster growers through a size of 60 mm SL and an age of 53 months. Growth rates of individual clams varied widely between time intervals. Correlation coefficient computed between initial SL (at planting) and growth was negative (-0.44) suggesting that smaller clams exhibited compensatory growth. These results are discussed in relation to the mechanisms of growth in clams and the development of protocols for selecting fast growing clams for culture.

The growth characteristics of hard clams, *Mercenaria mercenaria* (L.), throughout its geographical range have been determined (Ansell, 1968); however, very little information is available for South Carolina, Georgia and the east coast of Florida. In the early 1970's several investigations were initiated to provide information on growth of hard clams along the South Carolina coast (e.g. Eldridge *et al.*, 1976, 1979). Through a routine sampling program to determine the effects of increased population density on survival and growth of hard clams, considerable variation in size (growth) was observed. Variations in growth were not only observed under different environmental conditions (e.g. population density levels), but also among clams of the same age growing under apparently uniform conditions. In view of these observations, individual clams of known age were marked in order to monitor individual growth. A second objective of the study was to obtain an estimate of mortality without predation.

MATERIALS AND METHODS

In May 1975, hatchery seed clams approximately 5 months old and 13 mm in shell length, obtained from Coastal Zone Resources Corporation of North Carolina, were planted and held in Clark Sound, South Carolina until January 1976. At that time, clams were large enough (\bar{X} shell length = 24.7 mm) to be numbered with Testors' enamel paint on one shell valve and Sanford's Sharpie felt-tip pen on the other valve. A total of 313 clams were marked and measured for shell length (anterior-posterior axis, SL), shell height (dorso-ventral axis, SH) and shell width (lateral axis, SW) with vernier calipers to the nearest 0.1 mm (see Fig. 1).

Clams were planted in equal numbers (stocking density of approximately 226 clams/m²) in 2 oyster trays (118 X 61 X 14 cm) filled with 14 cm of natural sediment. Trays were supplied with protective lids made of 5-mm mesh plastic cloth and placed in a subtidal site that was approximately 0.5 m below mean low water. This area is characterized by mostly sand (20-30% silt-clay) and a salinity of 25-30 ‰ (Eldridge *et al.*, 1979).

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Clams were measured and trays cleaned 9 times over a 4.5 year period from January 1976 through May 1980. Each surviving clam was measured for SL, SH and SW, and if necessary, clams were renumbered with a felt-tip pen. Great care was taken to maintain the identity of individual clams. Clams that died during the study period were not replaced, but the numbers on their empty shells were recorded as an identity check on surviving clams.

Linear measurements were computed and compared using Statistical Analysis Systems (SAS-79) (Barr *et al.*, 1979). Specific statistical procedures (regression analysis, correlation coefficients, Kolmogorov's D statistic and χ^2 tests) used to analyze data are noted in the following section.

RESULTS

The means and standard deviations of the three shell dimensions measured are shown in Figure 1. The three shell dimensions exhibit similar growth patterns, and the relationships of SW and SH regressed against SL were linear (R^2 for $SH/SL = 0.97$; R^2 for $SW/SL = 0.99$). Since the shell proportions did not change over SL ranges used in this study, and SL has been extensively used in the past to report growth in *M. mercenaria* (Ansell, 1968 and references within), it was selected for further statistical analysis and presentation of results.

The number of surviving clams and the respective size distributions are shown in Figure 2. The calculated instan-

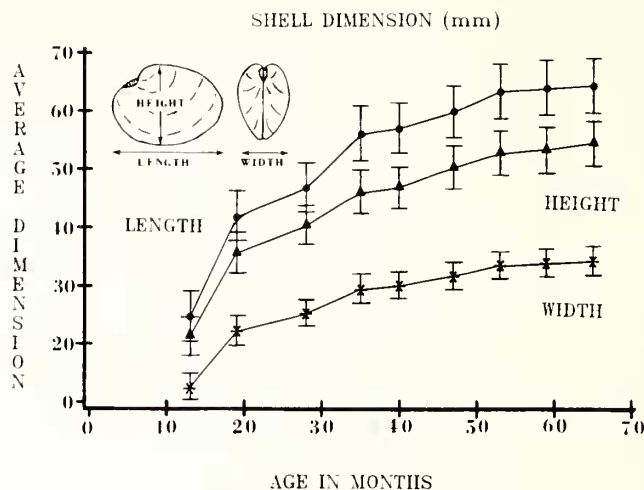


Fig. 1. Mean and standard deviations of shell length, height and width for clams grown in a subtidal location in South Carolina from January 1976 to May 1980. All shell dimensions in mm.

taneous mortality rate (Z) was 0.04, which translates into annual mortality rate 4.06% (Ricker, 1975). Approximately 50% of the total mortality, occurred in the interval between April and November, 1977. Nothing unusual happened during this time interval to explain the high mortality. It is possible

Table 1. Size-specific mean growth rates (Δ SL/month) by time intervals (age in months) for clams ($N = 266$) grown in a subtidal location in South Carolina from January 1976 to May 1980. Number of clams in each size-class interval in parenthesis.

Initial Size (mm)	Jan-Jul 1976 (13-19)	Jul-Apr 1977 (19-28)	Apr-Nov 1977 (28-35)	Nov-Apr 1978 (35-40)	Apr-Nov 1978 (40-47)	Nov-May 1979 (47-53)	May-Nov 1979 (53-59)	Nov-May 1980 (59-65)	Mean (13-65)
< 25.0	2.94 (130)								2.94 (130)
25.0-29.9	2.74 (111)								2.74 (111)
30.0-34.9	2.72 (24)	0.57 (11)	1.41 (2)						2.01 (37)
35.0-39.9	2.65 (1)	0.55 (67)	1.38 (7)						0.66 (75)
40.0-44.9		0.52 (130)	1.34 (83)	0.28 (1)	0.38 (1)				0.83 (215)
45.0-49.9		0.54 (50)	1.35 (119)	0.33 (21)	0.51 (11)	0.50 (4)	0.67 (1)	0.05 (1)	0.98 (207)
50.0-54.9		0.44 (8)	1.37 (48)	0.24 (92)	0.44 (81)	0.58 (31)	0.18 (7)	0.02 (4)	0.54 (271)
55.0-59.9			1.31 (7)	0.15 (94)	0.38 (108)	0.60 (103)	0.09 (57)	0.03 (45)	0.32 (414)
60.0-64.9				0.08 (47)	0.38 (52)	0.57 (90)	0.12 (102)	0.05 (103)	0.23 (394)
65.0-69.9				0.04 (11)	0.46 (13)	0.59 (34)	0.13 (75)	0.06 (83)	0.18 (226)
> 69.9						0.45 (4)	0.12 (24)	0.04 (30)	0.10 (58)
Mean	2.84 (266)	0.53 (266)	1.35 (266)	0.18 (266)	0.41 (266)	0.58 (266)	0.12 (266)	0.05 (266)	

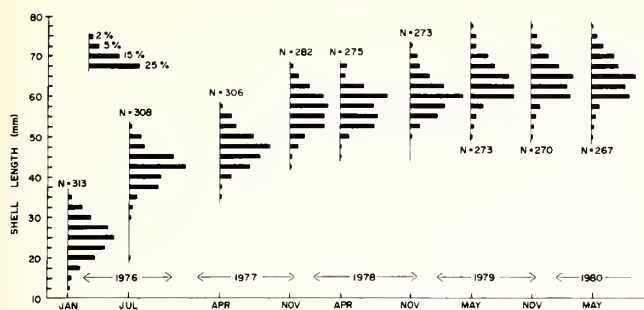


Fig. 2. Histograms show size (shell length) distributions of clams grown in a subtidal location in South Carolina from January 1976 to May 1980. Population size (N) listed adjacent to the histograms.

that some of the mortality was related to the sampling procedure, because April 1977 was the first time that clams were stored in a refrigerated room out of water during the measur-

ing process. During the previous measuring periods, clams were stored in saltwater aquaria. Some stress may have been associated with the transfer of clams from ambient water temperatures of 18-20°C to refrigerated room temperatures of 12-13°C and back to ambient temperatures over a 3-day period.

Of the 267 clams that survived to the end of the study, 266 clams had complete growth records. The individual with incomplete growth records was deleted from the data base and further statistical analysis. Growth (Δ SL/month) declined over the 4.5 year study period (Table 1). The first (Jan-Jul 1976) and the third time intervals (Apr-Nov 1977) had the greatest monthly incremental increase in SL.

Comparisons of growth (Δ SL/month) between size-class intervals within any time interval (columns in Table 1) indicated a general decrease with increased size. Growth was also observed to decrease with increased age. Comparisons of growth of the same size clams (e.g. 40.0-59.9 size-class

Table 2. Distribution (%) of 5-size categories by sampling data (age in months) for clams grown in a subtidal location in South Carolina from January 1976 to May 1980. Initial classification of size categories of class based on shell length at planting (Jan 1976).

Size Categories		Jan 1976 (13)	July 1976 (19)	Apr 1977 (28)	Nov 1977 (35)	Apr 1978 (40)	Nov 1978 (47)	May 1979 (53)	Nov 1979 (59)	May 1980 (65)
Very Small Clams (VS)	VS	100	69.8	62.3	47.2	43.4	35.8	26.4	28.3	28.3
	S	-	28.3	26.4	32.1	30.2	32.1	35.8	34.0	37.7
	M	-	1.9	7.6	9.5	11.3	13.2	17.0	15.1	13.2
	L	-	0.0	1.9	7.6	11.3	11.3	9.4	9.4	7.6
	VL	-	0.0	1.9	3.8	3.8	7.6	11.3	13.2	13.2
Small Clams (S)	VS	-	22.6	34.0	32.1	34.0	34.0	34.0	32.1	34.0
	S	100	45.3	35.8	35.8	32.1	26.4	24.5	20.8	18.9
	M	-	30.2	26.4	17.0	13.2	26.4	18.9	22.6	22.6
	L	-	1.9	3.8	15.1	20.8	9.4	20.8	22.6	22.6
	VL	-	0.0	1.9	0.0	0.0	3.8	1.9	1.9	3.8
Medium Sized Clams (M)	VS	-	7.6	3.8	13.2	13.2	11.3	17.0	17.0	17.0
	S	-	17.0	22.6	13.2	13.2	24.5	17.0	22.6	20.8
	M	100	37.7	34.0	28.3	28.3	18.9	26.4	22.6	24.5
	L	-	34.0	30.2	37.7	34.0	34.0	26.4	24.5	26.4
	VL	-	3.8	9.4	7.6	11.3	11.3	13.2	13.2	11.3
Large Clams (L)	VS	-	0.0	0.0	3.8	7.6	7.6	7.6	7.6	7.6
	S	-	9.4	5.7	7.6	9.4	11.3	17.0	17.0	15.1
	M	-	18.9	26.4	32.1	34.0	28.3	24.5	26.4	26.4
	L	100	47.2	39.6	22.6	17.0	24.5	20.8	20.8	22.6
	VL	-	24.5	28.3	34.0	34.0	28.3	30.2	28.3	28.3
Very Large Clams (VL)	VS	-	0.0	0.0	3.7	3.7	11.1	14.8	15.1	13.2
	S	-	0.0	11.1	11.1	14.8	5.6	5.6	5.6	7.6
	M	-	11.1	5.6	13.0	13.0	13.0	13.0	13.0	15.1
	L	-	16.7	24.1	16.7	16.7	20.4	22.2	22.2	20.8
	VL	100	72.2	59.3	55.6	51.8	50.0	44.4	44.4	44.4
Chi ² Value	-	-	292.02	204.4	140.95	115.89	88.17	62.56	58.04	63.01
d.f.	-	-	16	16	16	16	16	16	16	16
P.	-	-	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001

Chi ²(χ^2) test of association.

intervals or rows in Table 1) between the third (Apr-Nov 1977) and fifth time interval (Apr-Nov 1978) indicated that younger clams grew faster, approximately 4 times faster than older clams. This trend was especially noticeable when growth of clams in the sixth (Nov 1978 - May 1979) and last interval (Nov 1979 - May 1980) were compared. Growth of the younger clams (i.e. during sixth interval) was 10 times that of the older clams during the last time interval.

The relative position of individual clams in the size distribution was followed throughout the study. Individual clams surviving the study period (N = 266) were grouped into one of 5-size categories (very small, small, medium, large, and very large clams) according to an individual's SL and position in the size distribution in January 1976 (age 13 months). Each size category was allocated equal number of clams (53 clams per category) so that the 53 smallest clams

were categorized as very small, the next 53 clams as small, and so on. Table 2 gives the relative position (as a percentage) in the size distribution throughout the study of each of the initial size categories of clams. For example, clams classified as very small clams in January 1976 (100%) constituted 69.8% of the very small and 1.9% of the medium-sized clams in July 1976. By May 1980, only 28.3% remained in the very small category, while 13.2% were found among the very largest clams in the size distribution. Some very small and small clams caught up with larger individuals or compensated after 4.5 years of growth. However, a greater percentage of clams tended to maintain their relative positions in the size distribution. During the study, 24% and 19% of the individual clams remained within their respective size categories for 7 and 8 consecutive time intervals and 15% remained in their size category throughout the study. The χ^2 test of associa-

Table 3. Distribution (%) of 5-growth rate categories by time interval (age in months) for clams grown in a subtidal location in South Carolina from January 1976 to May 1980. Initial classification of clam growth rates based on rates between initial planting and first sampling data (Jan-Jul 1976).

Growth Rate Categories		Jan-Jul 1976 (13-19)	Jul-Apr 1977 (19-28)	Apr-Nov 1977 (28-35)	Nov-Apr 1978 (35-40)	Apr-Nov 1978 (40-47)	Nov-May 1979 (47-53)	May-Nov 1979 (53-59)	Nov-May 1980 (59-65)
Very Slow Growing Clams (VS)	VS	100	20.8	28.3	13.2	26.4	28.3	26.4	24.5
	S	-	20.8	20.8	13.2	13.2	26.4	24.5	15.1
	I	-	18.8	20.8	22.6	24.5	17.0	11.3	9.4
	F	-	17.0	15.1	28.3	15.1	13.2	17.0	15.1
	VF	-	22.6	15.1	22.6	20.8	15.1	20.8	35.8
Slow Growing Clams (S)	VS	-	15.1	24.5	20.8	20.8	20.8	20.8	20.8
	S	100	28.3	20.8	28.3	18.9	18.9	24.5	20.8
	I	-	13.2	20.8	15.1	28.3	15.1	24.5	28.3
	F	-	26.4	22.6	15.1	17.0	24.5	20.8	20.8
	VF	-	17.0	11.3	20.8	15.1	20.8	9.4	9.3
Intermediate Growing Clams (I)	VS	-	20.8	11.3	17.0	15.1	18.9	22.6	22.6
	S	-	11.3	22.6	26.4	28.3	22.6	18.9	26.4
	I	100	34.0	20.8	20.8	17.0	18.9	18.9	13.2
	F	-	18.9	20.8	13.2	20.8	18.9	17.0	20.8
	VF	-	15.1	24.5	22.6	18.9	20.8	22.6	17.0
Fast Growing Clams (F)	VS	-	22.6	17.0	24.5	20.8	17.0	15.1	20.8
	S	-	20.8	18.9	17.0	17.0	13.2	13.2	15.1
	I	-	18.9	26.4	24.5	17.0	24.5	24.5	22.6
	F	100	22.6	18.9	17.0	20.8	24.5	24.5	24.5
	VF	-	15.1	18.9	17.0	24.5	20.8	22.6	17.0
Very Fast Growing Clams (VF)	VS	-	20.4	18.5	24.1	16.7	14.8	14.8	11.1
	S	-	18.5	16.7	14.8	22.2	18.5	18.5	22.2
	I	-	14.8	11.1	16.7	24.1	24.1	20.4	18.5
	F	-	14.8	22.2	25.9	18.5	20.4	18.5	18.5
	VF	100	31.5	31.5	18.5	24.1	24.1	25.9	22.2
Chi ² Values		-	19.45	16.18	14.85	12.94	10.88	13.47	23.94
d.f.		-	16	16	16	16	16	16	16
P.		-	0.246	0.440	0.536	0.677	0.817	0.836	0.091

Chi² (χ^2) test of association.

tion indicated that a significant ($P \leq 0.0001$) association existed between the initial size-category classification of clams and their relative position in the size distribution after growing for various time periods. Thus, it appeared, the size (SL) the majority of clams obtained by their first year's growth was an indicator of their position in the size distribution in future years.

In an attempt to determine if growth in a particular time interval was equally as good an indicator as size (SL) of future growth, 5 categories of growth (very slow, slow, intermediate, fast and very fast) were classified according to an individual clam's growth performance. Initially, the 5 categories were based on the growth in the first time interval (Jan-Jul 1976) and traced through the remainder of the study period (Table 3). As a follow-up to these analyses, growth performance of individual clams were similarly scored, but an individual's growth category was reclassified according to its growth in the immediately preceding time interval so that the growth rate classification based on a single time interval did not bias our conclusions. Results from these analyses were almost identical to those done initially, and therefore, were not presented in tabular form. The χ^2 test values of association listed in Table 3 indicated little association existed between

growth in the first time interval (or any time interval) and growth in another interval. For example, clams which were very slow growers in the first time interval (Jan-Jul 1976) were distributed almost equally among the other growth categories (slow, intermediate, fast and very fast) by the next and following time intervals. Only 1.5% and 0.4% of the clams remained within their respective growth categories for 4 and 5 consecutive intervals; none remained in the same growth category after 6 consecutive intervals. An increased association indicated by a higher χ^2 value in the last time interval probably resulted from difficulties in determining which clams were slow and very slow growers when growth had slowed to a negligible rate (see Table 1).

Mean SL and growth (Δ SL) of the very slow growing and very fast growing categories of clams ($N = 53/\text{category}$) in each time interval are presented in Table 4. Individual clams in the very slow and very fast categories change their status from one time interval to the next, so the mean changes in SL cannot be simply added to the mean SL in one time interval to yield the mean SL in another interval. Very fast growing clams were consistently smaller than very slow growers through May 1979 (53 months age). Examination of Figure 2 indicated a slight departure from a normal distribution of SL at this time, but this departure was non-significant ($P > 0.05$) according to Kolmogorov's D statistic. Clams averaged approximately 60 mm SL at 53 months of age (Fig. 1).

Table 4. Mean initial shell length (SL in mm) and changes in SL (Δ SL) by time interval for the very slowest growing ($N = 53$) and very fastest growing clams ($N = 53$) held in a subtidal location in South Carolina from January 1976 to May 1980. Growth rate categories based on clams performance in the preceding time interval.

Time Intervals (age)	Very Slow Growers		Very Fast Growers	
	\bar{X} SL \pm SD	\bar{X} Δ SL \pm SD	\bar{X} SL \pm SD	\bar{X} Δ SL \pm SD
Jan-Jul 1976 (13-19)	25.8 \pm 4.17	14.0 \pm 1.12	23.0 \pm 4.28	20.2 \pm 0.97
Jul-Apr 1977 (19-28)	42.7 \pm 3.46	2.4 \pm 0.66	41.5 \pm 4.50	7.2 \pm 0.93
Apr-Nov 1977 (28-35)	46.8 \pm 4.24	6.7 \pm 0.84	46.5 \pm 4.64	12.4 \pm 1.05
Nov-Apr 1978 (35-40)	59.0 \pm 3.74	n.d.	53.9 \pm 4.04	2.5 \pm 1.04
Apr-Nov 1978 (40-47)	57.1 \pm 4.11	1.0 \pm 0.42	56.0 \pm 4.47	5.0 \pm 1.07
Nov-May 1979 (47-53)	60.3 \pm 5.06	1.7 \pm 0.54	59.6 \pm 4.97	5.4 \pm 0.61
May-Nov 1979 (53-59)	62.6 \pm 4.72	0.1 \pm 0.05	64.7 \pm 4.48	1.8 \pm 0.65
Nov-May 1980 (59-65)	62.9 \pm 4.94	n.d.	65.1 \pm 4.24	1.0 \pm 0.39

n.d. = no detectable growth.

DISCUSSION

Annual mortality rate of 4.06% approximates a previous estimate (1.43%) for larger clams held under similar conditions (Eldridge and Eversole, 1982). In both studies, experimental trays were covered with a plastic cloth to help protect clams from predators so these figures underestimate mortality. However, what these studies do indicate is that mortality of clams (≥ 24 mm SL) is quite low in absence of predation. Other potential mortality factors such as Hurricane David which moved up the coastline of South Carolina in September 1979 had little effect on survival of clams in the subtidal location. On the other hand, clams held in one experimental tray in an intertidal location as part of another study, approximately 15 m from the subtidal location and 0.3 m above mean low water, experienced nearly 100% mortality during Hurricane David (Eldridge and Eversole, 1982).

Decreased incremental growth with increased size (SL) has been reported for hard clams (e.g. Chestnut, 1952; Gustafson, 1955; Pratt and Campbell, 1956). However, contrary to previous studies, growth (Δ SL) of clams also appeared to decrease with age. The mechanisms suggested for reduced growth with increases in bivalve size (e.g. reduced gross growth efficiency, Bayne *et al.*, 1976) have not been adequately explored to explain growth reductions with increases in age or the possible interaction between age and size. Senility itself does not appear to be principal cause for reduced growth with increases in age, because growth in long-lived bivalves such as hard clams continue throughout life (Comfort, 1979 and references within).

Shell growth which is known to be highly variable in molluscs (Wilbur and Owen, 1964), has been observed to gradually decline in variability with age and/or size of bivalves (Weymouth *et al.*, 1931; Kristensen, 1957; Walne, 1958; Brown *et al.*, 1976; Wendell *et al.*, 1976). The decline has been attributed to either growth compensation (Ricker 1969) or greater mortality at the extremes of the size distribution (Brown *et al.*, 1976). Mortality in this study, however, was not restricted to any particular age or size, partly because the clams were protected from predators.

According to Ricker (1975), a negative correlation between growth and initial size indicates growth compensation or the process where smaller individuals catch up with larger individuals in an age class. Correlations coefficients between the variables of initial size and incremental growth (Δ shell dimension) were negative (-0.439 for SL; -0.435 for SH; and -0.443 for SW). If smaller clams were catching up with larger clams, the standard deviation about mean linear shell measurements shown in Figure 1 would be expected to diminish with age and growth. The standard deviations in this study, however, were relatively constant or increased slightly (e.g. the standard deviation for SL increased from 4.19 to 4.82 over the 4.5-year study period).

The degree of compensatory growth exhibited in this study can occur without a decrease in standard deviation because not all the small clams caught up with larger clams in the study period (4.5 years). Data in Table 2 show that a considerable proportion of those clams starting as very large, large, intermediate, small and very small clams occupy the same size category after 4.5 years growth. The range of sizes also remains very similar over the study period with a slight skewness in the size distribution toward larger sizes after May 1979 (Fig. 2). After May 1979, the SL of the very fast growers were larger than the slowest growers (Table 4). This may be the point (age and size) where some clams finally compensate for delayed initial growth and catch up with those clams with a head start on growth.

Evidence of this sort suggests that compensatory growth in molluscs may be more common place than previously thought. Those investigations where decreases in standard deviation have been reported (e.g. Kristensen, 1957; Walne 1958) were probably the most dramatic cases of growth compensation, if size selective mortality can be assumed not to be the principal causative factor. Crabs appear to exhibit some size selection when preying on hard clams (Whetstone and Eversole, 1978, 1981). A more complete picture of compensatory growth in molluscs relies on a good (valid) aging technique, a problem that has plagued malacologists for years, and a method of back calculation of body dimension similar to that used with fish (e.g. Carlander, 1981). Development of the acetate peel method of preparing shell sections (Rhoads and Lutz, 1980) and validation of this aging technique with bivalves (e.g. Ropes, 1984) will go a long way in resolving the problem of compensatory growth in molluscs.

As expected, individuals in designated shell-size categories (Table 2) remained quite constant where individuals in growth rate categories continuously changed dur-

ing the study (Table 3). Shell size is a history of past growth events and is less likely to change abruptly. Growth which is a dynamic process is continually being influenced by and responding to environmental, physiological and genetic factors. For example, Chanley (1959) observed that individual clams of similar genetic background grew well in one year and, then poorly in another year. He attributed this variation in shell growth to environmental factors, even though clams were reared under nearly identical conditions. Apparently, individual clams can rapidly change growth rates in response to microenvironmental factors which may not be readily obvious to the researcher. In our case, filtration rates and food uptake of individual clams may have been influenced by their position in the tray (e.g. edge vs. centrally located planting positions) which in turn could have influenced the growth of an individual.

Since clams were virtually the same age, differences in initial SL in January 1976 must have resulted from more rapid growth of some individuals during the growout phase from May 1975 to January 1976. Shell growth of individuals varied considerably over this 8-month period prior to marking in January. For example, at May 1975, a sample of 400 clams ranged from 9.9-16.8 mm SL and had mean SL of 13.0 mm (SD = 1.43) compared to a range of 11.7 to 35.3 mm SL and mean SL of 24.7 mm (SD = 4.19) in January 1976. If these differences in growth rate are due in part to genetic factors, then growth (size) could be used in designating individuals for selective breeding programs. The existence of growth differences at this size range or age, however, does not appear to provide the appropriate information from which to make the most reliable selections. Selection of the top 20% of the population, as fast growers when clams average 25 mm SL (and approximately 1 year of age) could result in considerable error. It is noteworthy, that less than 50% of the clams categorized as very large clams in January 1976 were very large after May 1979 (53 months of age) (Table 2). Also 33% of those originally classified as very large had growth such that they assumed positions in the size distribution equivalent to the intermediate, small and very small size categories by 53 months (Table 2).

Our data does not permit recommendations concerning specific size at which to begin picking the fastest growers for a selective breeding program. The probability of selecting the fastest growers increases with time and growth of clams, but it would be impractical and expensive for clam breeders to wait until clams reached 60 mm SL (and age of approximately 4 years in our situations) before selecting the fastest growers. Ideally, the selection process should be targeted for those clams which reach market size (approximately 45 mm SL) the fastest. We feel this may be best accomplished by selecting the fastest growers after clams have completed the rapid growth phase and have, hopefully, compensated for any slow start.

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LITERATURE CITED

- Ansell, A. D. 1968. The rate of growth of the hard clam *Mercenaria mercenaria* (L) throughout the geographical region. *Journal du Conseil Permanent International pour l'Exploration de la Mer* 31(3):364-409.
- Barr, A. J., J. H. Goodnight, J. P. Sall, H. W. Blair and D. M. Chilko. 1979. *SAS User's Guide*, 1979 edition. SAS Institute, Inc., Raleigh, NC, 494 pp.
- Bayne, B. L., R. J. Thompson and J. Widdows. 1976. Physiology I. In: *Marine Mussels*, B. L. Bayne, ed., pp. 121-206. Cambridge University Press, Cambridge, England, 506 pp.
- Brown, R. A., R. Seed and R. J. O'Connor. 1976. A comparison of relative growth in *Cerastoderma* (= *Cardium*) *edule*, *Modiolus modiolus*, and *Mytilus edulis* (Mollusca: Bivalvia). *Journal of Zoology (London)* 179:297-315.
- Carlander, K. D. 1981. Caution on the use of the regression method of back-calculating lengths from scale measurements. *Fisheries* 6(1):2-4.
- Chanley, P. E. 1959. Inheritance of shell markings and growth in the hard clam, *Venus mercenaria*. *Proceedings of the National Shellfisheries Association* 50:163-169.
- Chestnut, A. F. 1952. Growth rates and movements of hard clams, *Venus mercenaria*. *Proceedings of the Gulf and Caribbean Fisheries Institute* 4:49-59.
- Comfort, A. 1979. *The Biology of Senescence*. Elsevier North Holland Inc., New York, 414 pp.
- Eldridge, P. J., W. Waltz, R. C. Gracy and H. H. Hunt. 1976. Growth and mortality rates of hatchery seed clams, *Mercenaria mercenaria*, in protected trays in waters of South Carolina. *Proceedings of the National Shellfisheries Association* 66:13-20.
- Eldridge, P. J., A. G. Eversole and J. M. Whetstone. 1979. Comparative survival and growth rates of hard clams *Mercenaria mercenaria*, planted in trays subtidally and intertidally at varying densities in a South Carolina estuary. *Proceedings of the National Shellfisheries Association* 69:30-39.
- Eldridge, P. J. and A. G. Eversole. 1982. Compensatory growth and mortality of the hard clam, *Mercenaria mercenaria* (Linnaeus, 1758). *The Veliger* 24 (3):276-278.
- Gustafson, A. H. 1955. Growth studies in the quahog *Venus mercenaria*. *Proceedings of the National Shellfisheries Association* 45:140-150.
- Kristensen, I. 1957. Differences in density and growth in a cockle population in the Dutch Wadden Sea. *Archives Neerlandaises Zoologie* 12:351-453.
- Pratt, D. M. and D. A. Campbell. 1956. Environmental factors affecting growth in *Venus mercenaria*. *Limnology and Oceanography* 1(1): 2-17.
- Rhoads, D. C. and R. A. Lutz. 1980. *Skeletal Growth of Aquatic Organisms*. Plenum Press, New York, 750 pp.
- Ricker, W. E. 1969. Effects of size-selective mortality and sampling bias on estimates of growth mortality, production, and yield. *Journal of Fisheries Research Board of Canada* 26:479-541.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Bulletin of Fisheries Research Board of Canada* 191:1-382.
- Ropes, J. W. 1984. Procedures of preparing acetate peels and evidence validating the annual periodicity of growth lines formed in the shells of ocean quahogs, *Arctica islandica*. *Marine Fisheries Review* 46:27-35.
- Walne, P. R. 1958. Growth of oysters (*Ostrea edulis* L.) *Journal of the Marine Biological Association of the United Kingdom* 37:591-602.
- Wendell, F., J. D. Demartini, P. Dinnel and J. Siecke. 1976. The ecology of the gaper or horse clam, *Tresus capax* (Gould 1850) (Bivalvia: Mactridae), in Humboldt Bay, California. *California Fish and Game* 62(1):41-64.
- Weymouth, F. W., H. C. McMillin and W. H. Rich. 1931. Latitude and relative growth of the razor clam, *Siliqua patula*, Dixon. *Journal of Experimental Biology* 8:228-249.
- Whetstone, J. M. and A. G. Eversole. 1978. Predation on hard clams, *Mercenaria mercenaria*, by mud crabs, *Panopeus herbstii*. *Proceedings of the National Shellfisheries Association* 68:42-48.
- Whetstone, J. M. and A. G. Eversole. 1981. Effects of size and temperature on mud crab, *Panopeus herbstii*, predation on hard clams, *Mercenaria mercenaria*. *Estuaries* 4:153-156.
- Wilbur, K. M. and G. Owen. 1964. Growth. In: *Physiology of Mollusca*, Volume 1, K. M. Wilbur and C. M. Yonge, eds., pp. 211-242. Academic Press, New York, 473 pp.